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On the border of Europe and Asia: *Gobio uralensis*, a new species of gudgeons (Cypriniformes, Gobionidae) from the Caspian Sea basin

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Abstract

A new species of cypriniform fish was discovered during studies of the riverine fish fauna of the Caspian Sea basin, employing an integrative taxonomy approach. The Ural gudgeon is herein described as a new species from the Ural River system, which is considered a geographical boundary between Europe and Asia. The new species is distinguished from the other gudgeon species by a combination of morphological characters and genetic data. Morphologically, it is very similar to *Gobio volgensis* from the Volga basin. Genetically, however, it is closer to *G. acutipinnatus*, which occurs in the upper Irtysh River (Ob' River system), and to *G. multipunctatus* from the Lake Alakol basin in Central Asia (*p*-distance = 0.037; COI mtDNA). Therefore, the Ural gudgeon, which is endemic to the Ural River system, is of Asian rather than European origin. The biogeography of freshwater aquatic animals in the region is discussed in relation to paleogeographic events and connections between the Caspian Sea and Ob' drainages.

Key Words

Biogeography, DNA barcoding, endemics, freshwater fish, genetics, taxonomy

Introduction

According to modern taxonomic concepts, gudgeons of the genus *Gobio* Cuvier, 1816 (Gobionidae, Cypriniformes) comprise 47 valid species (Fricke et al. 2025; Fang et al. 2025). The genus *Gobio* Cuvier, 1816 (Gobionidae, Cypriniformes) is widely distributed across Eurasia. Its range extends from the Iberian Peninsula in the west, including Portugal, and covers most of Europe, except for the central and northern parts of the Scandinavian Peninsula, the Kola Peninsula, Northern Karelia, and the Arctic coast of European Russia. In the east, it reaches Korea and Sakhalin Island. The genus is also found in Siberian rivers, ranging from the Ural Mountains to the Lena and Kolyma river basins. However, it does not extend to the Arctic coast, with its northern limit around 65°N. In Southeast Asia, the range of *Gobio* includes China and extends westward along the southern border of Central Asia, encompassing northern Afghanistan and adjacent regions of the Middle East within the Caspian Sea basin. The range also includes the Caucasus and Asia Minor in the southwest (Bănărescu and Nalbant 1973; Fricke et al. 2025).

The type species *Gobio gobio* (Linnaeus, 1758) was, until recently, considered a morphologically variable species comprising several subspecies and intraspecific forms, distributed across much of Northern Eurasia, from the Iberian Peninsula to the Far East and northeastern Siberia (Berg, 1949; Bănărescu et al. 1999). However, revisions of European fishes have been proposed based on

phylogenetic (Kottelat 1997) and evolutionary (Mayden 2002) species concepts. It has been hypothesized that multiple distinct gudgeon species exist under the name *G. gobio*. A comprehensive revision of the genus cannot be resolved through examination of museum material – often old and poorly preserved – but requires direct comparison of freshly collected, well-preserved specimens (Kottelat 1997; Mayden 2002). Subsequently, based on morphological, karyological, and molecular genetic data, several gudgeon species within the genus *Gobio* were described as new (Vasil'eva et al. 2004, 2005, 2023; Doadrio and Madeira 2004; Freyhof and Naseka 2005; Kottelat and Persat 2005; Naseka et al. 2006; Xie 2007; Mendel et al. 2008; Turan et al. 2012, 2016, 2017, 2018; Li 2015). Additionally, molecular genetic analyses have confirmed the validity of several other species within the genus and revealed the hybrid origin of some populations (Doadrio and Madeira 2004; Yang et al. 2006; Mendel et al. 2008; Tang et al. 2011; Takács et al. 2014, 2021; Aksu and Bektaş 2019; Sheraliev et al. 2020; Zangl et al. 2020; etc.).

As part of efforts to document the ichthyofauna of Russia, we investigated gudgeons of the genus *Gobio* in the Ural River basin and adjacent drainage systems. The Ural River, the third longest river in Europe, has a total length of 2,428 km and a catchment area of 231,000 km^2. It flows through Russia and Kazakhstan, representing the boundary between Europe and Asia. The river originates in the Ural Ridge of the Southern Urals and drains into the northeastern Caspian Sea (Davydov 1936).

Studies of *Gobio* gudgeons in the Ural River basin have a history spanning more than a century. The earliest record of gudgeons in the region appears in Kessler (1877), who cited *Gobio fluviatilis* Cuvier, 1842 (now considered a junior synonym of *G. gobio*). Subsequent researchers (Navozov 1912; Berg 1914; Bening 1938; Tikhiy 1938; Kozhin 1949; Shaposhnikova 1964; Mitrofanov 1988; Zinovyev and Baklanov 2007; Magazov and Rechkalov 2007; Chibilev and Debelo 2009; Shevchenko 2018) reported the presence of *G. gobio* in the Ural River and its tributaries. Notably, *Gobio volgensis* Vasil'eva, Mendel, Vasil'ev, Lusk & Lusková, 2008 – originally described from the Volga River basin (Mendel et al. 2008) – was also reported from the Ural River delta (Bogutskaya et al. 2013). Based on comparative morphological analysis, Martynova and Vasil'eva (2021) assigned gudgeons from six populations in the Ural River basin to *G. volgensis*.

Based on a study of gudgeons from various parts of the Ural River basin, Shaposhnikova (1964) demonstrated their morphological heterogeneity. According to her observations, the population inhabiting the upper reaches of the Ural River is morphologically closer to gudgeons (identified as *G. gobio*) from the Northern Dvina basin (part of the Arctic Ocean catchment in European Russia), which are now referred to as *G. volgensis* (our data). In contrast, the population from the steppe tributaries of the middle Ural River more closely resembles the Siberian gudgeon *Gobio sibiricus* Nikolsky, 1936 – identified in the cited work as *Gobio gobio cynocephalus* Dybowski, 1869 – from the Ob' and Yenisei basins. Subsequent authors (Mitrofanov 1988; Chibilev and Debelo 2009) also suggested that gudgeons from the Ural River basin differ from typical *G. gobio*, although no dedicated studies have been conducted to confirm this.

Thus, the taxonomy of gudgeons from the Ural River basin remains unresolved, with all previous conclusions based solely on morphological data. In the absence of molecular genetic data, there is insufficient evidence to determine whether the Ural gudgeons belong to any of the species inhabiting adjacent basins. Our study, based on extensive sampling and an integrative taxonomic approach, enabled us to formally describe the Ural gudgeons as a distinct species.

Materials and methods

Sampling

Material for this study was collected by the authors in the Ural River basin and adjacent basins of the Volga and Ob' rivers in Russia during 2020–2021. Sampling sites are shown in Fig. 1. Type specimens and additional material of the newly described species were collected from nine localities in the Ural River basin. Comparative material was collected from basins adjacent to the Ural River. *G. volgensis* specimens were obtained from four localities in the Volga River basin, and *G. sibiricus* from three localities in the Ob' River basin. Additionally, *Gobio acutipinnatus* Menshikov, 1939, from Kazakhstan was included in the comparative material, comprising a type series (syntypes) from Lake Markakol (Menshikov 1939), deposited in the Zoological Institute of the Russian Academy of Sciences. Sample characteristics are provided in the subsequent description of the new species and comparative remarks.

Fish were caught using a frame net and a seine net with a mesh size of 6–8 mm. Individuals were euthanized in a solution of clove oil and photographed in an aquarium under artificial lighting. Photographs were taken using a Nikon D5300 camera with a Nikkor 60mm f/2.8G lens (Nikon Corporation, Tokyo, Japan), and a physical white swatch was used for color correction. Tissues (pectoral or pelvic fins) were taken from some specimens (DNA vouchers) and placed in 96% ethanol for subsequent DNA extraction in the laboratory. Then, most of the specimens were preserved in 10% formalin, while some (usually small individuals) were preserved in 96% ethanol. In the laboratory, formalin samples were rinsed in running water and then transferred to 70% ethanol.

The types (holotype, some paratypes), additional, and comparative material were deposited at the Fish Collection of the Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences, Borok, Russia (**IBIW_FS**); the remaining paratypes (see below) were deposited at the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (**ZISP**), and the Zoological Museum of the Moscow State University, Moscow, Russia (**ZMMU**).

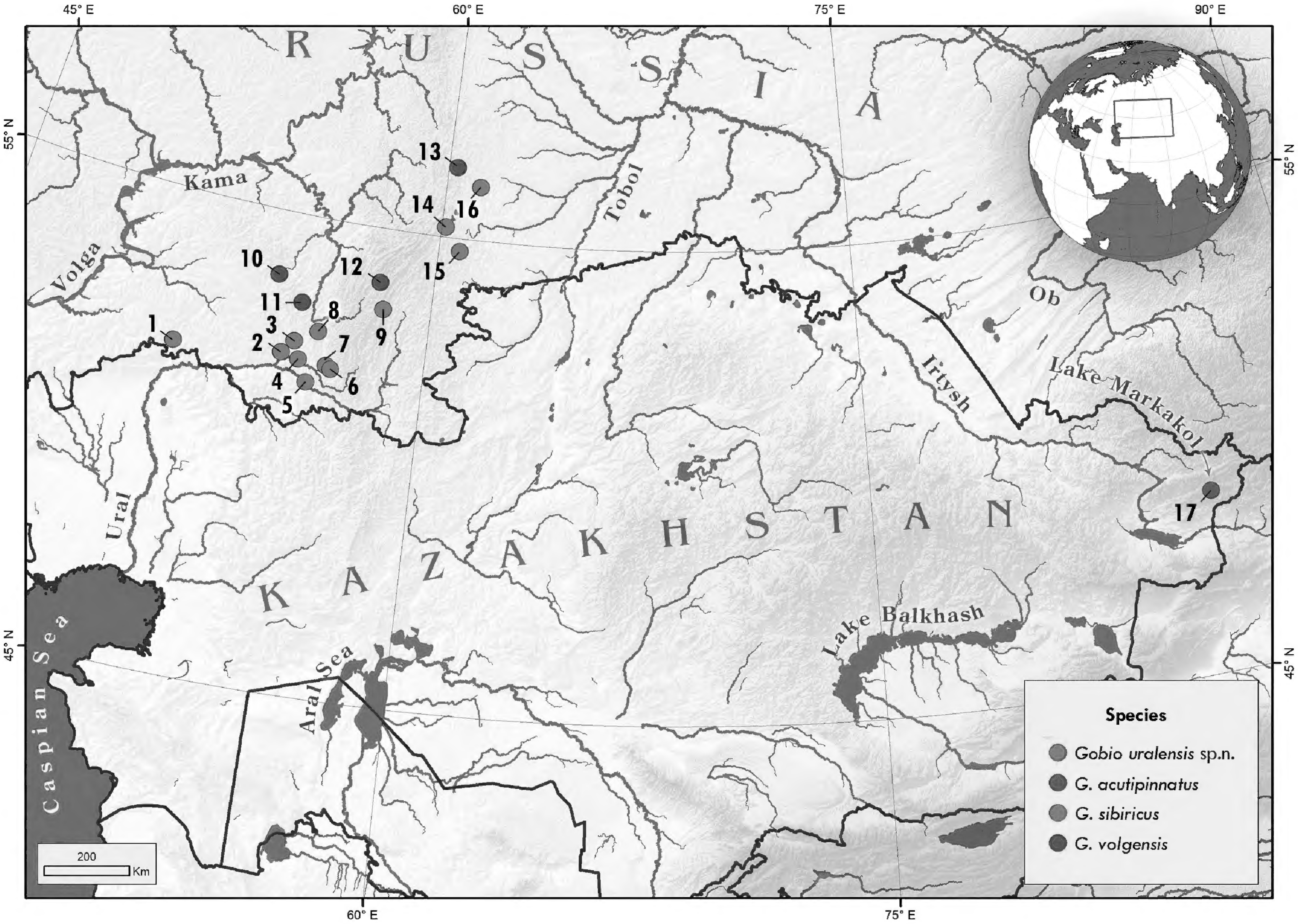

Figure 1. Map of localities of *Gobio* spp. sampled for this study: 1. Bolshoy Kizil River; 2. Chagan River; 3. Ural River; 4. Sakmara River; 5. Kargalka River; 6. Bolshoy Yushatyr River; 7. Nakas River; 8. Uskalyk River; 9. Assel River; 10. Dyoma River; 11. Ashkadar River; 12. Belaya River; 13. Chusovaya River; 14. Kushtumga River; 15. Koelga River; 16. Sinara River; 17. Lake Markakol.

Comparative material

Gobio volgensis: • 6 spec. (IBIW_FS_467) 101.1–129.7 mm SL, Russia, Sverdlovsk Region, Polevskoy Distr., near Kosoy Brod, Chusovaya River, 56.4799°N, 60.3270°E, 23 Aug. 2020, O.N. Artaev, A.A. Bolotovskiy, I.V. Pozdeev, I.S. Turbanov leg. • 4 spec. (IBIW_FS_468) 92.4–117.3 mm SL, same data (see above), 29 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 1 spec. (IBIW_FS_469) 98.8 mm SL, 1 spec. (IBIW_FS_470) 79.5 mm SL, Russia, Republic of Bashkortostan, Beloretsky Distr., near Sermenevo, Belaya River, 53.8679°N, 58.0977°E, 24 Aug. 2020, O.N. Artaev, A.A. Bolotovskiy, I.V. Pozdeev, I.S. Turbanov leg.• 26 spec. (IBIW_FS_471) 67.4–100.8 mm SL, Russia, Republic of Bashkortostan, Fyodorovsky Distr., near Zlataustovka, Ashkadar River, 53.1802°N, 55.5203°E, 26 Aug. 2020, O.N. Artaev, A.A. Bolotovskiy, I.S. Turbanov leg. • 8 spec. (IBIW_FS_472) 68.8–87.4 mm SL, Russia, Republic of Bashkortostan, Miyakinsky Distr., near Kanbekovo, Dyoma River, 53.6641°N, 54.5435°E, 27 Aug. 2020, O.N. Artaev, A.A. Bolotovskiy, I.S. Turbanov leg. ***Gobio sibiricus***: • 1 spec. (IBIW_FS_473) 78.1 mm SL, 12 spec. (IBIW_FS_474) 24.0–62.4 mm SL, Russia, Chelyabinsk Region, Miass Distr., near Severnye Pechi, Kushtumga River, 55.2105°N, 60.1570°E, 23 May 2020, O.N. Artaev, A.A. Bolotovskiy, I.V. Pozdeev, I.S. Turbanov leg. • 10 spec. (IBIW_FS_477) 54.6–84.4 mm SL, Russia, Chelyabinsk Region, Chebarkulsky Distr., near Zvyagino, Koelga River, 54.7327°N, 60.7620°E, 27 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 13 spec. (IBIW_FS_475) 53.0–94.7 mm SL, 3 spec. (IBIW_FS_476) 40.8–56.7 mm SL, Russia, Chelyabinsk Region, Kaslinsky Distr., near Bulzi (abandoned Yugo-Konevo), Sinara River, 56.1209°N, 61.2691°E, 27 May 2021 O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. ***Gobio acutipinnatus***: Syntypes • 7 spec. (ZISP 26865) 82.2–102.9 mm SL, Kazakhstan, East Kazakhstan Region, Kurshim Distr., Lake Markakol, ca. 48.7555°N, 85.7642°E, 21 July 1936, M.I. Menshikov leg. • 3 spec. (ZISP 7831) 101.79–110.21 mm SL, same locality (see above), 1887, Suworcev leg.

Morphological studies

Morphological and morphometric characters were selected based on previous studies on the taxonomy of the genus *Gobio* (Bănărescu et al. 1999; Vasil'eva et al. 2004; Freyhof and Naseka 2005). A total of 18 meristic characters and 31

morphometric indices, along with several proportional relationships and two qualitative characters, were investigated. Individual measurements were taken as described by Hubbs and Lagler (1946). All measurements were taken point-to-point using a digital caliper and recorded to the nearest 0.1 mm by a single operator to ensure consistency, following the recommendations of Mina et al. (2005). Standard length (SL) was measured from the tip of the snout to the end of the hypural complex. Lateral head length (HL) was measured to include the skin flap. All indices are given as percentages of standard length (SL) unless otherwise noted.

External meristic characters were counted on both sides. The count of lateral line scales includes all pored scales, from the first one just behind the supracleithrum to the posterior-most scale on the caudal-fin base (hypural). The total number of lateral line scales, as well as the transverse scales above and below the lateral line, were counted. These correspond to horizontal scale rows located below the origin of the dorsal fin and above the origin of the pelvic fin, respectively. The last two branched rays, articulated on a single pterygiophore in the dorsal and anal fins, are noted as "1½". For the description of the type and additional material of new species, the number of unbranched rays in the dorsal and anal fins was counted. The number of outer gill rakers on the first gill arch was counted on the right side of the specimens. Meristic characters (except for the axial skeleton) and qualitative characters (breast squamation and coloration) were examined using an MC-2-ZOOM stereomicroscope (Micromed, Saint Petersburg, Russia). Axial skeleton was examined using radiographs. Vertebral counts were made following Naseka (1996), using PRDU (v.II) X-ray equipment (ELTECH-Med, St. Petersburg, Russia). Images of pharyngeal teeth were obtained using a JEOL JSM-6510LV scanning electron microscope (JEOL, Tokyo, Japan). Abbreviations used are **A** – number of branched rays of anal fin, **D** – number of branched rays of dorsal fin, **P** – number of branched rays of pectoral fin, **V** – number of branched rays of pelvic fin, **LLt** – total number of lateral line scales, **LL** – number of lateral line scales to hypural, **GR** – number of gill rakers on the outer side of the first gill arch, **up LL** – number of scales above lateral line in horizontal rows below the dorsal fin origin, **down LL** – number of scales between lateral line and the pelvic fin origin, **CPS** – number of circumpeduncular scales, **Vert.** – total vertebrae, Va – abdominal vertebrae, **VpreD** – predorsal abdominal vertebrae, **Vi** – intermediate vertebrae, **Vc** – caudal vertebrae, **VpreA** – preanal caudal vertebrae, **VpostA** – postanal caudal vertebrae.

Statistical procedures were carried out with the R statistics using packages: *ggplot2*, *rstatix*, *tidyverse*, and *MASS*. The pattern of morphological variation was analyzed using Linear Discriminant Analysis (LDA). The results of LDA were assessed using the Wilks' Lambda and F-test statistics. The significant differences in morphometric and meristic characters were tested using the Kruskal-Wallis test followed by Dunn's post hoc test with Bonferroni correction.

In total, morphological analysis was performed on 170 specimens: *G. volgensis* – 46, *G. sibiricus* – 37, *G. acutipinnatus* – 10 (7 for radiographs), and new species – 77 specimens.

Molecular and phylogenetic study

DNA was isolated by the salt-extraction method (Aljanabi and Martinez 1997) from ethanol-fixed tissues. Molecular genetic studies were conducted on 58 samples: new species – 29, *G. volgensis* – 23, *G. sibiricus* – six specimens (see Suppl. material 1). As comparative phylogenetic material, we obtained six COI sequences from several other *Gobio* species (*G. cynocephalus*, *G. macrocephalus* Mori, 1930, *G. multipunctatus* Vasil'eva, Mamilov & Sharakhmetov, 2023, *G. holurus* Fowler, 1976, *G. krymensis* Bănărescu & Nalbant, 1973, and *G. sarmaticus* Berg, 1949) as well as included sequences from GenBank – *G. cynocephalus*, *G. nigrescens* (Keyserling, 1861), *G. macrocephalus*, *G. artvinicus* Turan, Japoshvili, Aksu & Bektaş, 2016, *G. caucasicus* Kamensky, 1901, *G. acutipinnatus*, *G. kizilirmakensis* Turan, Japoshvili, Aksu & Bektaş, 2016, *G. sakaryaensis*, *G. lozanoi*, *G. occitaniae*, *G. holurus*, *G. lepidolaemus*, *G. sibiricus*, *G. ohridanus*, *G. skadarensis* Karaman, 1937, *G. gobio*, *G. balcanicus* Dimovski & Grupche, 1977, *G. bulgaricus* Drensky, 1926, *G. kovatschevi* Chichkoff, 1937 and *G. volgensis* (Triantafyllidis et al. 2011; Geiger et al. 2014; Knebelsberger et al. 2015; Mousavi-Sabet et al. 2016; Yang et al. 2016; Corse et al. 2017; Friedrich et al. 2018; Li et al. 2018; Aksu and Bektaş 2019; Sheraliev et al. 2020; Yi and Fu 2020; Behrens-Chapuis et al. 2021; Sheraliev and Peng 2021; and unpublished sequences in GenBank – https://www.ncbi.nlm.nih.gov/) (see Suppl. material 1).

Mitochondrial cytochrome *c* oxidase subunit I (COI mtDNA) barcode region was amplified using M13-tailed primer cocktail: FishF2_t1: 5′-TGT AAA ACG ACG GCC AGT CGA CTA ATC ATA AAG ATA TCG GCA C-3′, FishR2_t1: 5′-CAG GAA ACA GCT ATG ACA CTT CAG GGT GAC CGA AGA ATC AGA A-3′, VF2_t1: 5′-TGT AAA ACG ACG GCC AGT CAA CCA ACC ACA AAG ACA TTG GCA C-3′, and FR1d_t1: 5′-CAG GAA ACA GCT ATG ACA CCT CAG GGT GTC CGA ARA AYC ARA A-3′ (Ivanova et al. 2007). PCR conditions for COI followed protocols from Ivanova et al. (2007).

Sequencing of the PCR products purified by ethanol and ammonium acetate (3 M) precipitation was conducted using the Applied Biosystems 3500 DNA sequencer (Thermo Fisher Scientific, USA) with primers M13F 5′-GTA AAA CGA CGG CCA GT-3′ M13R-pUC 5′- CAG GAA ACA GCT ATG AC-3′ for COI.

DNA chromatograms were checked for errors in FinchTV 1.4.0 (Rothgänger et al. 2006), and the DNA sequences were aligned using the ClustalW algorithm in MEGA7 (Kumar et al. 2016). Phylogenetic analysis was performed on COI (627 bp) sequences. Only unique haplotypes were used in downstream phylogenetic analyses.

The Bayesian phylogenetic analysis was performed in a Bayesian statistical framework implemented in BEAST v.1.10.4 (Hill and Baele 2019) with 2×10^7 MCMC generations (10% burn-in) and parameters sampled every 2000 steps. The substitution models by codon position for Bayesian analysis were selected in PartitionFinder v.2.1.1 (Lanfear et al. 2016) with the greedy algorithm (Lanfear et al. 2012) (Suppl. material 2). Maximum likelihood phylogenies were inferred using IQ-TREE v.2.2.0 (Nguyen et al. 2015) in PhyloSuite v.1.2.3 (Zhang et al. 2020; Xiang et al. 2023) under the Edgelinked partition model for 1000 ultrafast (Minh et al. 2013) bootstraps. ModelFinder v.2.2.0 (Kalyaanamoorthy et al. 2017) in PhyloSuite v.1.2.3 was used to select the best-fit partition model (edge-linked) using the AICc criterion (Suppl. material 2).

The average intra-group as well as the average pairwise intergroup *p*-distances using concatenated COI sequences data set were calculated using the MEGA7 program (Kumar et al. 2016) with 1000 bootstrap replicas.

Map visualization

The map was created using the QGIS software v.3.34. Digital elevation model visualized based on GMTED2010, 30 sec. resolution (Danielson and Gesch 2011); river systems – HydroATLAS v.1.0 (Linke et al. 2019).

Results

Phylogenetic relationships and genetic distance

The phylogenetic Bayesian tree of the genus *Gobio* shows (Fig. 2) that the gudgeon from the Ural River basin forms its own lineage and is a sister (with a high support) to *G. acutipinnatus* from the upper Irtysh River and its tributaries (Ob' River basin, Arctic Ocean catchment) and *G. multipunctatus* from the Emel River (Lake Alakol basin; enclosed water system). Genetic *p*-distances to these species are 0.037 ± 0.007 and 0.037 ± 0.008, respectively (Table 1). Being combined together, the aforementioned species form a clade that is sister to a clade of the Caucasian species *G. caucasicus* from the Kura River (Caspian Sea basin) and *G. artvinicus* from the Chorokh (Çoruh) and Natanebi rivers (Black Sea basin) – although this node is weaker supported. ML-tree (Suppl. material 3) supported the same phylogenetic relationships of the Ural gudgeon, *G. acutipinnatus*, *G. multipunctatus*, and *G. caucasicus-artvinicus* lineages. The results obtained confirm that the Ural gudgeon is an independent new species.

Noteworthy, this new species is genetically distant from geographically neighboring species – *G. volgensis* from the Volga River basin (*p*-distance = 0.059 ± 0.009) and *G. sibiricus* from the rivers of the Ob' River basin (0.047 ± 0.008) (Table 1). Intraspecific divergence of the Ural gudgeon (0.001) is comparable to that in other species (Table 1). Below we provide a description of this species.

Systematics

Class Actinopteri Cope, 1871
Order Cypriniformes Bleeker, 1859
Family Gobionidae Bleeker, 1863
Genus *Gobio* Cuvier, 1816

Gobio uralensis sp. nov.

https://zoobank.org/25D6334F-3234-4D62-A90D-4B4C85C4BB0F
Figs 3, 4, 8A
(English name – Ural gudgeon, Russian name – уральский пескарь)

Gobio fluviatilis non Cuvier, 1842 – Kessler 1877: 298.

Gobio gobio (non Linnaeus, 1758) – Navozov 1912: 263; Berg 1914: 428 (part.); Bening 1938: 237; Tikhiy 1938: 307; Berg 1949: 640 (part.); Kozhin 1949: 374 (part.); Shaposhnikova 1964: 78; Mitrofanov 1988: 6, fig. 1 (part.); Kottelat 1997: 60 (part.); Bănărescu et al. 1999: 81 (part.); Zinovyev and Baklanov 2007: 54 (part.); Magazov and Rechkalov 2007: 87 (part.); Chibilev and Debelo 2009: 101 (part.); Shevchenko 2018: 122–123.

Gobio volgensis non Vasil'eva, Mendel, Vasil'ev, Lusk & Lusková, 2008 – Bogutskaya et al. 2013: 176, figs 35a, 36a (part.); Martynova and Vasil'eva 2021: 529 (part.), figs 1, 2; Vasil'eva et al. 2023: 503 (part.).

Type material. ***Holotype*** • (IBIW_FS_454) 97.7 mm SL, Russia, Republic of Bashkortostan, Abzelilovsky Distr., near Ryskuzhino, Bolshoy Kizil River, 53.3161°N, 58.3351°E, 24 Aug. 2020, O.N. Artaev, A.A. Bolotovskiy, I.V. Pozdeev, I.S. Turbanov leg. ***Paratypes*** • 4 spec. (IBIW_FS_455) 70.3–110.4 mm SL, 3 spec. (ZISP 57042) 69.8–73.4 mm SL, 3 spec. (ZMMU P-24633) 68.1–75.7 mm SL, same data as holotype.

Additional material. • 7 spec. (IBIW_FS_456) 40.9–64.4 mm SL, same data as holotype and paratypes • 4 spec. (IBIW_FS_457) 34.8–42.7 mm SL, Russia, Orenburg Region, Pervomaysky Distr., near Lyashevo, Chagan River, 51.8514°N, 51.4965°E, 22 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 1 spec. (IBIW_FS_458) 72.5 mm SL, Russia, Orenburg Region, Saraktashsky Distr., near Krasnogor, Ural River, 51.5591°N, 56.1224°E, 23 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 5 spec. (IBIW_FS_459) 38.9–50.3 mm SL, 32 spec. (IBIW FS_465) 27.9–39.9 mm SL, Russia, Orenburg Region, Saraktashsky Distr., near Nikolskoe, Sakmara River, 52.0018°N, 55.7371°E, 24 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 2 spec. (IBIW_FS_460) 85.0–87.5 mm SL, Russia, Orenburg Region, Sakmarsky Distr., near Svetlyi, Kargalka River, 52.0835°N, 55.1283°E, 24 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 11 spec. (IBIW_FS_461) 47.2–80.2 mm SL • 15 spec. (IBIW FS_466) 33.7–47.6 mm SL, Russia, Orenburg Region, Oktyabrsky Distr., Oktyabrskoe, Bolshoy Yushatyr River, 52.3631°N, 55.5008°E, 24 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 1 spec. (IBIW_FS_462) 71.8 mm SL, Russia, Republic of Bashkortostan, Kugarchinsky Distr., near Aznagulovo, Nakas River, 52.6431°N, 56.2436°E, 24 May 2021, O.N.

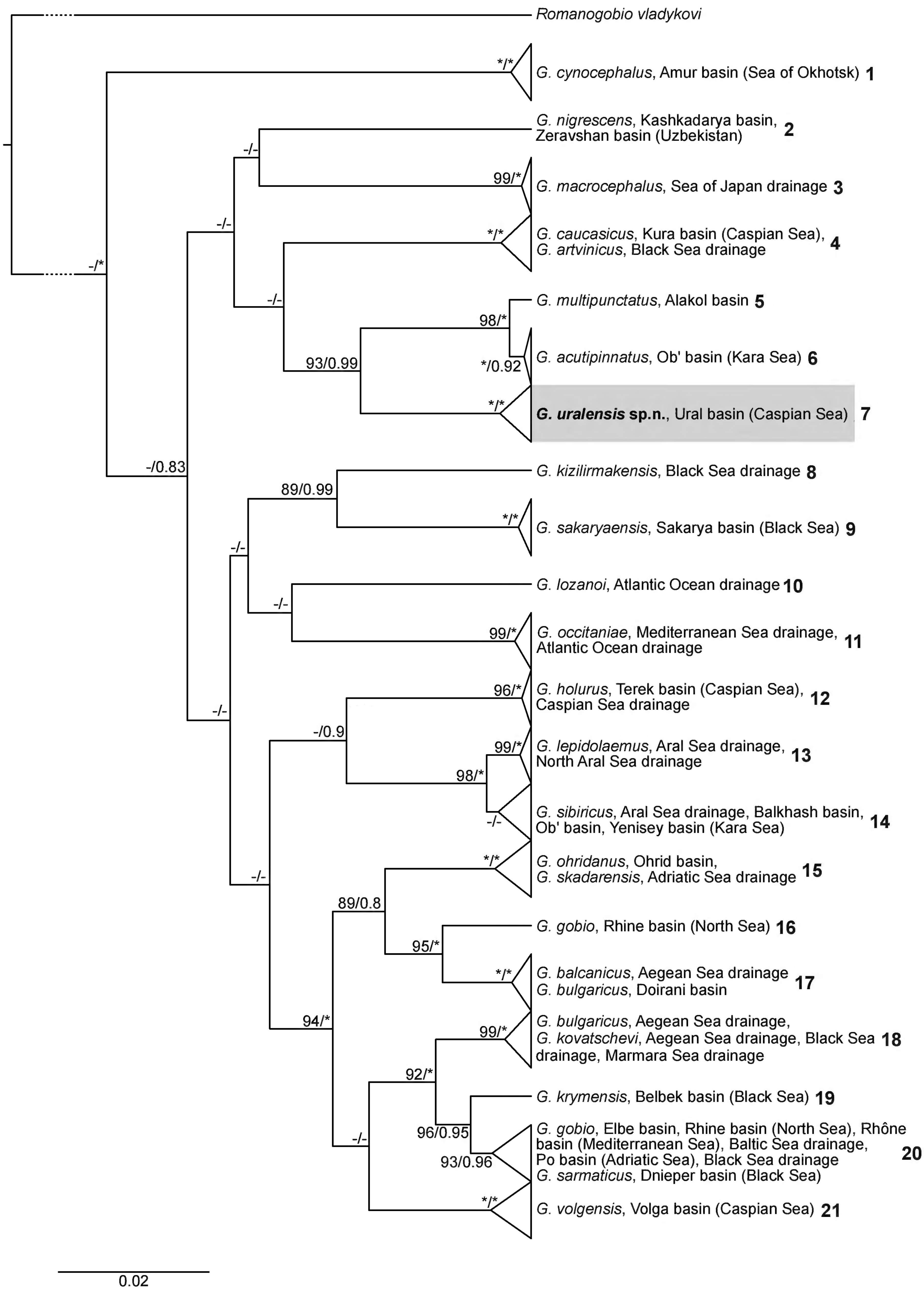

Figure 2. BI consensus tree of COI mtDNA sequences representing all available *Gobio* species in GenBank combined with our data set. *Gobio uralensis* sp. nov. is highlighted by color. Bootstrap values/posterior probabilities above 80/0.8 are shown; asterisks represent 100/1 bootstrap/posterior probability values. The scale bar is in expected substitutions per site. The nodes with multiple specimens collapsed to a triangle, with the horizontal depth indicating the level of divergence within the node. Lineage numbers are given by the bold numbers from 1 to 21.

Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 17 spec. (IBIW_FS_463) 57.9–82.1 mm SL, Russia, Republic of Bashkortostan, Zianchurinsky Distr., near Verkhniy Muinak, Uskalyk River, 51.9687°N, 56.6878°E, 25 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg. • 5 spec. (IBIW_FS_464) 37.2–81.4 mm SL, Russia, Republic of Bashkortostan, Zianchurinsky Distr., upstream Itkulovo, Assel River, 51.9047°N, 56.8683°E, 25 May 2021, O.N. Artaev, A.A. Bolotovskiy, A.V. Kutuzov leg.

Etymology. The adjective *uralensis* comes from the name of the Ural River, which literally means lives in the basin of this river.

Diagnosis. *Gobio uralensis* sp. nov. is distinguished by a combination of characters, none of which is unique, as follows: predorsal length 47.4–52.6% SL; postdorsal length 36.3–42.1% SL; body depth 17.4–23.7% SL; prepelvic length 49.8–56.8% SL; preanal length 70.2–75.2 SL; snout length 40.9–48.8% HL; interorbital width 22.3–29.6% HL; ratio of caudal peduncle length to caudal peduncle depth 2.0–2.8; pharyngeal teeth in two rows, 3.5–5.3; anal fin branched rays $6^1/_2$; number of lateral line scales 39–45, mean 42.1; 12 (mode) predorsal vertebrae; the breast between the pectoral fins is naked; lower lip is interrupted in middle, with a notch between narrower anterior and widening posterior parts.

Description. General appearance shown in Fig. 3. Morphometric and meristic data are given in Tables 2–4. Largest recorded specimen – 110.4 mm SL.

Morphometrics. The body and the caudal peduncle are moderately compressed; the minimum body depth is somewhat greater than the width of the caudal peduncle at the level of the last anal ray. Predorsal length is somewhat more than postdorsal length. The distance between pectoral and pelvic-fin origins is somewhat more than the distance between pelvic and anal-fin origins. The anus is closer to the insertion of the anal fin than to the origin of the pelvic fins; the pelvic fin reaches beyond the anus. Barbels are moderately long; they are usually less than 1/3 of the head length and reach up to the middle of the eye but never reach to its posterior edge. Paired fins are moderately long: pectoral fins never reach the pelvic fin insertion; ventral fins never reach the anal fin insertion. The eye is large with a diameter of 17.6–25.2% of the head length, an eye diameter of 2.2–3.3 times in head depth, and 1.0–1.5 times in interorbital width. The snout is pointed; its length is somewhat longer than the postorbital length. Caudal peduncle is 2.0–2.8 times longer than depth.

Meristics. Dorsal fin margin is concave, with 3 unbranched and $7^1/_2$ branched rays (only one specimen had $8^1/_2$ rays); anal fin margin is concave or straight, with 3 unbranched and $6^1/_2$ branched rays; pectoral fin branched ray numbers vary within 13–17 (mode 16 and 15 in left and right, respectively); and pelvic fin branched ray numbers vary within (5) 6–8 (mode 7). The shape of the caudal fin is variable; the two lobes are sharpened or rounded, with a notch in the middle. Body is covered by scales. Lateral line includes 39–45 total scales (mode 42) and 11–15 circumpeduncular scales (mode 12). Two-five gill rakers (modes 4 and 5) on outer side of first gill arch. Pharyngeal teeth are in two rows, 3.5–5.3, slightly hooked at tip (Fig. 4).

Total vertebrae 39–42 (mode 40), 20–22 (mode 21) abdominal, including 11–13 predorsal and 18–21 (mode 19) caudal, including 1–3 preanal and 16–19 postanal vertebrae. The radiograph of the holotype is given in Fig. 5.

Qualitative characters. The breast in front of the posterior edge of the base of the pectoral fins usually lacks scales; some individuals have 1–3 scales along the midline towards the throat [character state 1 following Naseka et al. (2006)] (Fig. 8A).

Coloration. Body is dark olive-brown above, merging into a light silvery underside. There are large, more or less rounded 6–14 (often 10) blotches on flank located along the lateral line. The color of the fins corresponds to the color of the body with several rows of small dark dots on the dorsal and caudal fins. Live coloration is given in Figs 3A, D, E, 8A.

Distribution. The type specimens were collected from the Bolshoy Kizil River, a tributary of the Ural River, near Ryskuzhino (53.3161°N, 58.3351°E), Republic of Bashkortostan, Russia (see Fig. 6). All other gudgeons genetically confirmed as the same species were caught in different locations in the Ural River basin (see materials). Although we suppose that the whole Ural River basin is inhabited by the Ural gudgeon, one may not exclude that some parts of the extended Ural drainage are inhabited by other species. According to Shaposhnikova (1964), the gudgeon is widespread throughout the Ural River. The gudgeon is especially abundant in the mountain tributaries of the Ural and in its upper reaches, where it is numerous in riffles and sandbanks; this is partly confirmed by the data of Martynova and Vasil'eva (2021) as well as by our observations.

Biology. In the Ural River near Orenburg, the gudgeon spawns from the middle of the twentieth days of April to early or mid-May, but individual spawning specimens are caught throughout the summer (Navozov 1912). Spawning is multiple (Shaposhnikova 1964). In all areas of the Ural basin, regardless of the time of year, larvae of Tendipedidae (Insecta: Diptera) are the main food item beginning from the first year of life. In addition, larvae of Heleidae (Insecta: Diptera), Oligochaeta (Annelida), larvae of Ephemeroptera (Insecta), Gastropoda (Mollusca), plant remnants, and diatom algae were also detected. In juveniles (up to 47 mm), Cladocera and Copepoda (Crustacea) as well as diatoms and other algae predominated in the food bolus (Shaposhnikova 1964).

Comparative remarks. As we have already noted above, in the earliest faunal studies, the gudgeons from the Ural River basin were identified as *Gobio gobio*. However, according to the latest data, *G. gobio* is distributed in the basins of the Atlantic Ocean, the North, Baltic and White Seas (including Great Britain and the upper Danube basin), but not in the Caspian Sea basin (Dyldin et al. 2023). At the same time, *G. gobio* is well differentiated from *G. uralensis* sp. nov. by a narrow lower lip with no interception between the anterior and posterior parts (vs. the lower lip is interrupted in the middle, with

Table 1. Genetic *p*-distances between *Gobio* spp. for COI mtDNA sequences. The averages of interspecies distances are given below the diagonal, the standard errors are given above the diagonal, and the intraspecies divergence is given in a diagonal in bold. Lineage numbers (from 1 to 21) are given in parentheses after the species name.

	***G. acutipinnatus* (6)**	***G. artvinicus* (4)**	***G. balcanicus* (17)**	***G. bulgaricus* (18)**	***G. bulgaricus* (17)**	***G. caucasicus* (4)**	***G. cynocephalus* (1)**	***G. gobio* (16)**	***G. gobio* (20)**	***G. holurus* (12)**	***G. kizilirmakensis* (8)**	***G. kovatschevi* (18)**	***G. krymensis* (19)**
G. acutipinnatus (6)	**0.001**	0.008	0.009	0.009	0.009	0.008	0.010	0.009	0.009	0.008	0.009	0.009	0.009
G. artvinicus (4)	0.049	**0.004**	0.008	0.008	0.008	0.002	0.009	0.008	0.008	0.008	0.008	0.008	0.008
G. balcanicus (17)	0.056	0.051	**0.003**	0.002	0.008	0.008	0.010	0.006	0.007	0.008	0.009	0.007	0.007
G. bulgaricus (18)	0.058	0.049	0.003	—	0.008	0.008	0.010	0.006	0.007	0.009	0.009	0.007	0.007
G. bulgaricus (17)	0.056	0.051	0.041	0.043	—	0.008	0.009	0.008	0.005	0.009	0.009	0.003	0.006
G. caucasicus (4)	0.048	0.004	0.049	0.049	0.049	**0**	0.009	0.008	0.008	0.008	0.008	0.008	0.008
G. cynocephalus (1)	0.074	0.062	0.073	0.071	0.068	0.063	**0.005**	0.010	0.009	0.009	0.009	0.009	0.009
G. gobio (16)	0.060	0.048	0.022	0.022	0.038	0.046	0.069	—	0.007	0.008	0.009	0.007	0.007
G. gobio (20)	0.053	0.042	0.032	0.034	0.019	0.040	0.062	0.029	**0.000**	0.008	0.008	0.004	0.003
G. holurus (12)	0.050	0.049	0.052	0.053	0.053	0.047	0.069	0.047	0.046	**0.002**	0.008	0.009	0.008
G. kizilirmakensis (8)	0.063	0.053	0.061	0.059	0.054	0.056	0.065	0.059	0.050	0.052	—	0.008	0.008
G. kovatschevi (18)	0.053	0.045	0.035	0.037	0.006	0.043	0.061	0.035	0.013	0.049	0.048	**0**	0.005
G. krymensis (19)	0.055	0.049	0.032	0.035	0.021	0.048	0.065	0.033	0.008	0.047	0.046	0.014	—
G. lepidolaemus (13)	0.048	0.046	0.048	0.049	0.050	0.045	0.068	0.050	0.044	0.041	0.057	0.047	0.045
G. lozanoi (10)	0.061	0.053	0.056	0.057	0.062	0.051	0.069	0.053	0.056	0.057	0.065	0.056	0.054
G. macrocephalus (3)	0.046	0.047	0.050	0.052	0.055	0.045	0.077	0.047	0.044	0.051	0.066	0.052	0.050
G. multipunctatus (5)	0.004	0.047	0.053	0.054	0.053	0.046	0.073	0.056	0.050	0.050	0.059	0.049	0.051
G. nigrescens (2)	0.071	0.067	0.075	0.077	0.067	0.065	0.080	0.070	0.061	0.065	0.065	0.064	0.059
G. occitaniae (11)	0.055	0.047	0.049	0.049	0.049	0.046	0.069	0.048	0.046	0.047	0.048	0.043	0.043
G. ohridanus (15)	0.061	0.057	0.033	0.035	0.045	0.056	0.076	0.038	0.038	0.057	0.064	0.040	0.037
G. sakaryaensis (9)	0.069	0.052	0.066	0.069	0.056	0.053	0.082	0.065	0.057	0.061	0.048	0.053	0.057
G. sarmaticus (20)	0.053	0.041	0.032	0.033	0.019	0.040	0.061	0.029	0.000	0.045	0.049	0.013	0.008
G. sibiricus (14)	0.048	0.042	0.044	0.046	0.043	0.041	0.063	0.044	0.038	0.035	0.052	0.040	0.039
G. skadarensis (15)	0.061	0.054	0.032	0.032	0.040	0.053	0.074	0.035	0.035	0.053	0.061	0.035	0.037
G. uralensis sp. nov. (7)	0.037	0.045	0.056	0.057	0.054	0.043	0.077	0.059	0.052	0.055	0.060	0.054	0.056
G. volgensis (21)	0.064	0.059	0.037	0.038	0.042	0.056	0.073	0.045	0.031	0.055	0.065	0.035	0.034

a groove between narrower anterior and wider posterior parts in *G. uralensis* sp. nov.); its minimum body depth always exceeds 30% of the length of the head and 40% of the length of the caudal peduncle (Vasil'eva et al. 2023).

Geographically, the two species closest to the new species are the Siberian gudgeon *G. sibiricus* (Figs 7C, D, 8C), distributed from the Ob' to Lena basins (including the Nura River in Kazakhstan), and *G. volgensis* (Figs 7A, B, 8B), known from the Volga River basin.

In turn, the new species is morphologically almost indistinguishable from the Volga gudgeon; therefore, the Ural populations were previously identified as *G. volgensis* (Vasil'eva et al. 2023). According to the materials of this study, *G. volgensis* from the Chusovaya, Belaya, Ashkadar and Dema rivers (neighboring rivers of the Volga River basin to the typical habitats of the Ural gudgeon) have a slightly higher total number of lateral line scales – a range 41–45 and median of 42.5 (vs. a range 39–45, median of 42 in *G. uralensis* sp. nov.), as well as a higher number of scales above lateral line – a range 5–6.5 and median of 6 (vs. a range 4–6, median of 5.5 in *G. uralensis* sp. nov.). Besides, small differences in the mean values of some morphometric characters are observed between the combined samples of both species (see Table 3).

Contrast to *G. uralensis* sp. nov. the minimum body depth in *G. sibiricus*, always exceeds 30% of the length of the head and 40% of the length of the caudal peduncle (vs. usually exceeds the half of caudal peduncle length) and the number of blotches on flank along the lateral line in this species varies from 6 to 11 (vs. usually less than 10) (Vasil'eva et al. 2023). In addition, according to the materials of the present study, *G. sibiricus* from the Kushtumga, Koelga, and Sinara rivers (neighboring rivers of the Ob' River basin to the typical habitats of the Ural gudgeon) has a fewer number of lateral line scales to hypural and total number of lateral line scales (ranges 36–40 and 40–43, medians 39 and 42, respectively, vs. ranges 36–42 and 39–45, medians 37.5 and 41 in *G. uralensis* sp. nov.) and a smaller number of predorsal vertebrae (range 11–13, median 12 vs. range 10–12, median 11 in *G. uralensis* sp. nov.). Besides, small differences in the mean values of some morphometric characters are observed between the combined samples of both species (see Table 3).

Table 1. Continued.

	G. lepidolaemus (13)	*G. lozanoi* (10)	*G. macrocephalus* (3)	*G. multipunctatus* (5)	*G. nigrescens* (2)	*G. occitaniae* (11)	*G. ohridanus* (15)	*G. sakaryaensis* (9)	*G. sarmaticus* (20)	*G. sibiricus* (14)	*G. skadarensis* (15)	*G. uralensis* sp. nov. (7)	*G. volgensis* (21)
G. acutipinnatus (6)	0.009	0.009	0.008	0.002	0.010	0.009	0.010	0.010	0.009	0.008	0.009	0.008	0.010
G. artvinicus (4)	0.008	0.008	0.008	0.008	0.009	0.008	0.009	0.009	0.008	0.007	0.009	0.008	0.009
G. balcanicus (17)	0.008	0.009	0.008	0.009	0.010	0.009	0.007	0.010	0.007	0.008	0.006	0.009	0.007
G. bulgaricus (18)	0.008	0.009	0.009	0.009	0.010	0.009	0.007	0.010	0.007	0.008	0.006	0.009	0.007
G. bulgaricus (17)	0.009	0.009	0.009	0.009	0.009	0.008	0.008	0.010	0.005	0.008	0.007	0.009	0.008
G. caucasicus (4)	0.008	0.008	0.008	0.008	0.009	0.008	0.009	0.009	0.008	0.007	0.009	0.008	0.009
G. cynocephalus (1)	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.009	0.009	0.010	0.010	0.010
G. gobio (16)	0.009	0.008	0.008	0.009	0.010	0.008	0.007	0.010	0.007	0.008	0.007	0.009	0.008
G. gobio (20)	0.008	0.009	0.008	0.009	0.009	0.008	0.007	0.010	0.000	0.008	0.007	0.009	0.007
G. holurus (12)	0.008	0.009	0.008	0.008	0.009	0.008	0.009	0.009	0.008	0.007	0.009	0.008	0.009
G. kizilirmakensis (8)	0.009	0.009	0.009	0.009	0.009	0.008	0.010	0.008	0.008	0.008	0.009	0.009	0.009
G. kovatschevi (18)	0.009	0.009	0.008	0.009	0.009	0.008	0.008	0.009	0.004	0.008	0.007	0.009	0.007
G. krymensis (19)	0.009	0.009	0.008	0.009	0.009	0.008	0.008	0.010	0.003	0.008	0.007	0.009	0.007
G. lepidolaemus (13)	**0.002**	0.009	0.009	0.009	0.010	0.009	0.009	0.010	0.008	0.003	0.009	0.008	0.008
G. lozanoi (10)	0.061	**0**	0.009	0.009	0.010	0.008	0.010	0.009	0.009	0.009	0.009	0.009	0.010
G. macrocephalus (3)	0.060	0.068	**0.002**	0.008	0.009	0.008	0.009	0.010	0.008	0.008	0.008	0.009	0.009
G. multipunctatus (5)	0.051	0.057	0.045	—	0.010	0.009	0.010	0.010	0.009	0.008	0.009	0.007	0.010
G. nigrescens (2)	0.066	0.075	0.066	0.067	**0**	0.010	0.011	0.011	0.009	0.009	0.010	0.010	0.010
G. occitaniae (11)	0.058	0.051	0.047	0.051	0.069	**0.003**	0.009	0.009	0.008	0.008	0.009	0.009	0.009
G. ohridanus (15)	0.056	0.067	0.058	0.057	0.080	0.057	**0**	0.010	0.007	0.009	0.003	0.010	0.008
G. sakaryaensis (9)	0.067	0.061	0.068	0.065	0.083	0.056	0.067	**0.003**	0.010	0.009	0.010	0.010	0.010
G. sarmaticus (20)	0.043	0.056	0.044	0.049	0.061	0.046	0.038	0.057	—	0.008	0.007	0.009	0.007
G. sibiricus (14)	0.008	0.054	0.054	0.047	0.061	0.052	0.050	0.061	0.038	**0.002**	0.008	0.008	0.008
G. skadarensis (15)	0.051	0.065	0.055	0.057	0.077	0.055	0.008	0.065	0.035	0.045	**0.004**	0.009	0.007
G. uralensis sp. nov. (7)	0.048	0.067	0.057	0.037	0.070	0.059	0.067	0.070	0.051	0.047	0.064	**0.001**	0.009
G. volgensis (21)	0.048	0.070	0.061	0.060	0.077	0.059	0.044	0.066	0.031	0.043	0.041	0.059	**0.003**

LDA analysis explained 86.88% of shape variations by the first LD axis and 13.12% by the second LD axis for all specimens of three species examined above. LDA of morphometric characters shows that *G. uralensis* sp. nov. together with *G. volgensis* is strongly different from *G. sibiricus* by LD1 in the following features: length caudal peduncle/depth caudal peduncle, interorbital length/eye diameter, and depth caudal peduncle/SL (Fig. 9). *Gobio uralensis* sp. nov. is slightly overlapping with *G. volgensis* by LD2 in the following features: head depth through nape/eye diameter, interorbital length/eye diameter, and length caudal peduncle/depth caudal peduncle. Specimens of *G. volgensis* are located mainly on the positive side of LD2, while specimens of *G. uralensis* sp. nov. are situated mainly on the negative side of LD2. The statistic values for LDA were as follows: Wilks' Lambda = 0.037001, approx. $F (62, 160) = 10.835$, $p < 0.0001$, indicating good species discrimination. Coefficients of linear discriminants see Suppl. material 4.

Further morphological comparison with a number of geographically close gudgeon species distributed out of the Volga and Ob' basins has been done based on literature data (except for *G. acutipinnatus*, some features of which were studied by authors using materials from the ZISP collection).

Another gudgeon species indicated in the literature for the Ob' River basin is *G. acutipinnatus* (Fig. 7E). This species was described from Lake Markakul in the Irtysh basin in Kazakhstan but today is also recorded for the water bodies of Russia, Mongolia, and China (Kottelat 2006; Yang et al. 2016; Yi and Fu 2020; Fricke et al. 2025). Compared to *G. acutipinnatus* from Lake Markakul (ZISP collection, 10 specimens), based on the materials of this study, *G. uralensis* sp. nov. has significantly (Kruskal-Wallis test, see Table 4) more pectoral fin branched rays, median 15.5 (vs. median 14.25), more total lateral line scales, median 42 (vs. median 41.5), and fewer scales below lateral line, median 3.75 (vs. median 4).

Compared to *G. lepidolaemus* Kessler, 1872 from the Zeravshan and Syr-Darya rivers based on the materials of Nikolsky (1936), *G. uralensis* sp. nov. has a greater number of lateral line scales (39–45, mean 42.1 vs. 36–42, mean 39.6) and anal fin branched rays $6^1/_2$ (vs. $5^1/_2$).

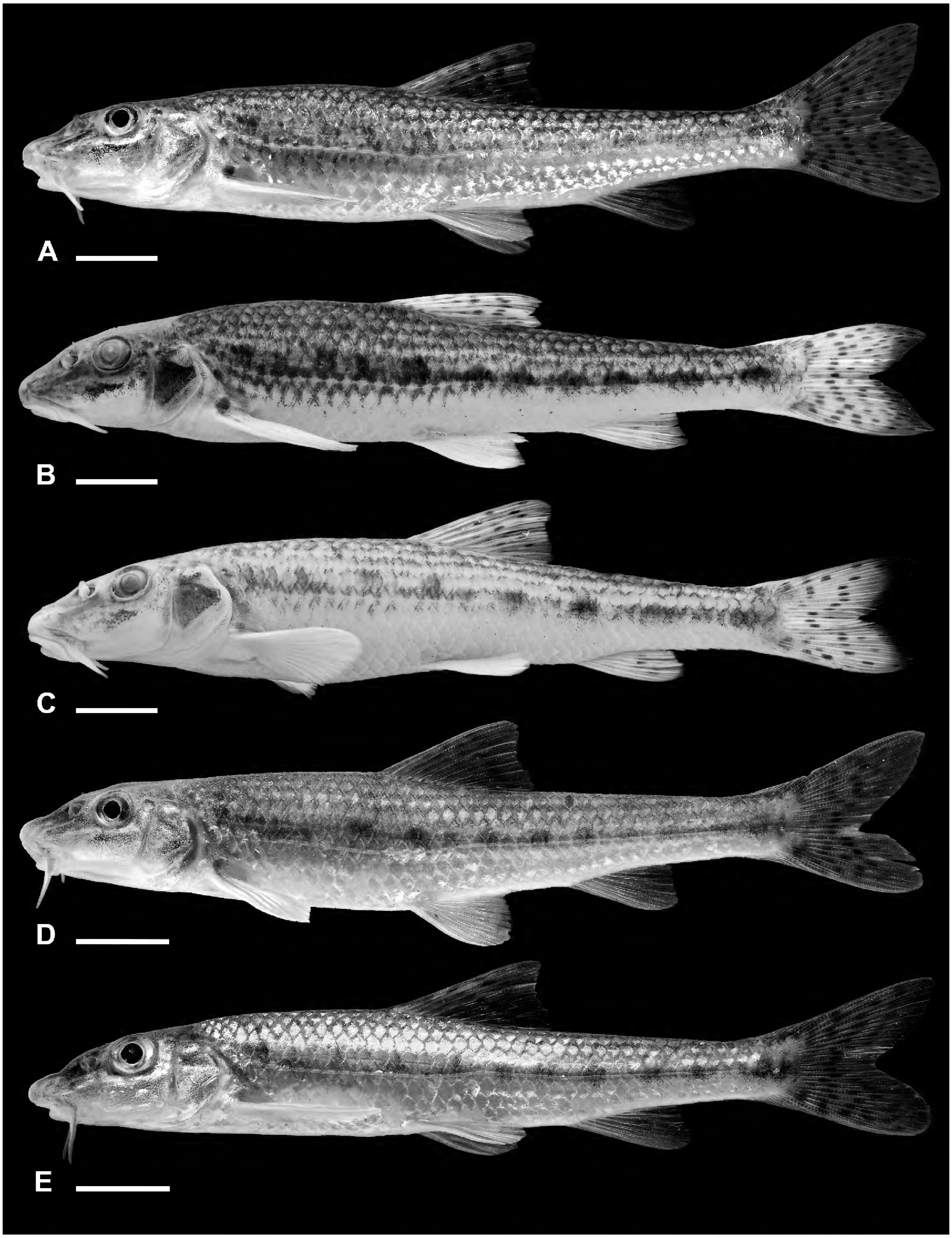

Figure 3. Lateral view of *Gobio uralensis* sp. nov.: **A–C.** Bolshoy Kizil River near Ryskuzhino (**A, B.** Holotype; **C.** Paratype); **D.** Uskalyk River near Verkhniy Muinak; **E.** Ural River near Krasnogor (right side, inverted image). **A, D, E.** Live coloration; **B, C.** After fixation in 10% formalin (5 months), then transferred to 70% ethanol. Scale bar: 10 mm.

Compared to *Gobio nigrescens* from the Hari River based on the materials of Mousavi-Sabet et al. (2016), *G. uralensis* sp. nov. has longer head (as % of SL) 25.6–30.0 (vs. 22.3–25.8), more predorsal lenght 47.4–52.6 (vs. 43.3–45.4), more prepelvic length 49.9–56.8 (vs. 46.4–50.7), and more preanal length 70.2–75.2 (vs. 67.1–69.1), less depth of caudal peduncle 7.2–8.8 (vs. 8.3–9.3), less body width 12.7–17.8 (vs. 17.3–18.7), has shorter cau-

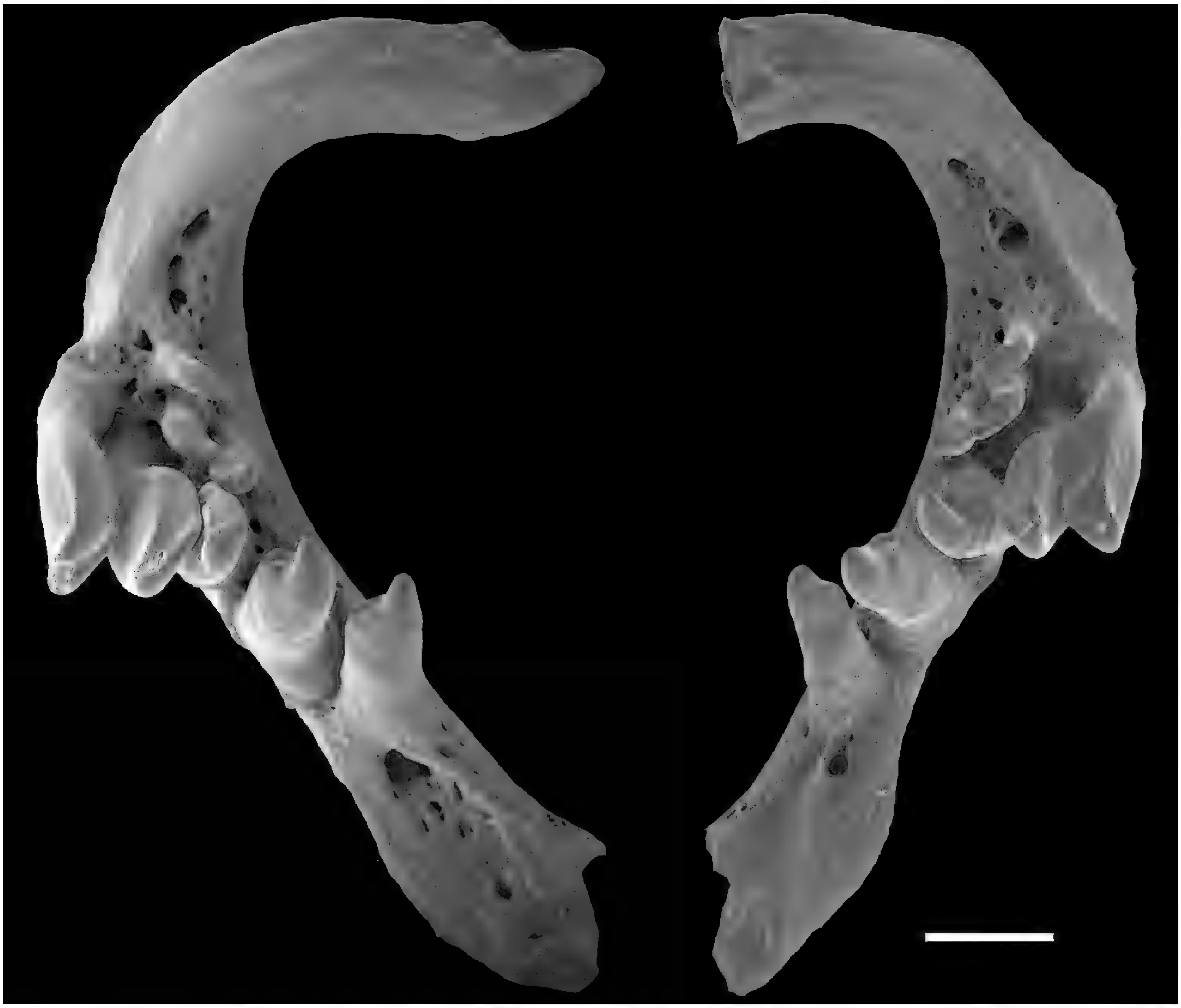

Figure 4. Dentition of pharyngeal bones (3.5–5.3) of *Gobio uralensis* sp. nov. Scale bar: 0.5 mm.

Figure 5. Radiograph of *Gobio uralensis* sp. nov., holotype: Scale bar: 10 mm.

dal peduncle 16.3–22.8 (vs. 21–24), has less head depth (in percent of HL) 52.6–62.0 (vs. 65–69), less interorbital width (in percent of HL) 22.3–29.6 (vs. 34–41), more snout length (in percent of HL) 40.9–48.8 (vs. 35–40), less anal fin branched rays $6^1/_2$ (vs. $5^1/_2$) and less circumpeduncular scales 11–15 (vs. 16).

Compared to *Gobio latus* Anikin, 1905 from Lake Issyk-Kul based on the materials of Berg (1949), *G. uralensis* sp. nov. has more numbers of pharyngeal teeth in minor row – 3.5–5.3 (vs. 2.5–5.2).

Compared to *Gobio multipunctatus* from the Emel River, Lake Alakol basin based on the materials of Vasil'eva et al. (2023), *G. uralensis* sp. nov. has less depth of caudal peduncle 7.2–8.8 (vs. 8.0–10.0), shorter caudal peduncle 16.3–22.8 (vs. 20.2–24.9), less dorsal fin depth 18.2–23.1 (vs. 21.8–26.2), more number of pharyngeal teeth in mi-

Table 2. Morphometric data of *Gobio uralensis* sp. nov. (holotype and paratypes, n = 11).

Character	holotype	paratypes			
		mean	min	max	SD
SL (mm)	97.7	77.9	70.3	110.4	–
In percent of SL:					
Head length (HL)	27.4	27.4	26.4	28.6	0.72
Body depth at dorsal-fin origin	18.3	19.1	18.3	19.9	0.51
Depth of caudal peduncle	7.8	8.0	7.3	8.5	0.34
Body width at dorsal-fin origin	14.7	15.4	14.7	16.2	0.47
Width of caudal peduncle at posterior anal-fin ray	8.2	8.5	7.7	9.2	0.47
Predorsal length	49.8	49.6	47.4	52.2	1.35
Postdorsal length	39.5	39.6	36.6	42.1	1.40
Prepelvic length	52.8	52.6	50.4	54.3	1.21
Preanal length	73.6	73.0	70.2	74.6	1.20
Distance between pectoral and pelvic-fin origins	26.7	26.8	26.0	29.0	0.90
Distance between pelvic and anal-fin origins	22.0	20.9	19.3	22.2	1.05
Distance between anus and anal-fin origin	7.7	7.8	6.8	8.8	0.67
Caudal peduncle length	21.0	20.5	19.0	21.9	0.87
Dorsal-fin base length	11.8	12.6	11.8	13.8	0.69
Dorsal-fin depth	20.4	20.3	18.2	21.1	0.77
Anal-fin base length	8.1	7.4	6.7	8.0	0.49
Anal-fin depth	15.2	15.7	14.9	17.3	0.75
Pectoral fin length	20.0	19.4	17.5	21.1	1.07
Pelvic fin length	16.0	15.5	13.9	16.4	0.69
In percent of HL:					
Head depth at nape	57.5	57.0	54.5	58.6	1.12
Head depth at eye	45.5	46.9	45.4	49.3	1.34
Snout length	41.8	43.7	40.9	46.6	1.86
Eye diameter	19.0	19.7	18.1	21.7	1.05
Postorbital distance	40.0	41.6	39.9	45.0	1.70
Maximum head width	58.6	59.4	56.5	62.1	1.54
Interorbital width	26.5	25.9	22.3	29.6	2.05
Barbel length	22.8	23.1	17.5	28.0	2.92
Ratios:					
Interorbital width/eye diameter	1.4	1.3	1.2	1.5	0.08
Snout length/eye diameter	2.2	2.2	1.9	2.6	0.19
Head depth at nape/eye diameter	3.0	2.9	2.7	3.2	0.16
Caudal peduncle length/depth	2.7	2.6	2.2	2.8	0.16

nor row – 3.5–5.3 (vs. 2.5–5.2), and has less black blotch numbers on body—often 10 (vs. usually more than 12).

Compared to *Gobio holurus* from the rivers of the western part of the Caspian basin based on the materials of Freyhof and Naseka (2005), *G. uralensis* sp. nov. has a naked breast between the pectoral fins (vs. the scaled breast). Compared to *G. holurus* from the Podkumok and Sunzha rivers (Berg 1914), *G. uralensis* sp. nov. has longer head (as % of SL) 25.6–30.0 (vs. 23.8–24.7), less postdorsal length 36.3–42.1 (vs. 42.6–43.1), more dorsal fin depth 18.2–23.1 (vs. 16.1–17.9), more anal fin depth 14.9–18.0 (vs. 13.9–14.1), and more ratio of caudal peduncle length to caudal peduncle depth 2.0–2.8 (vs. 1.9–2.0).

Discussion

According to our study, the Ural River basin is inhabited by a distinct species, *Gobio uralensis* sp. nov., currently known only from this riverine basin (Fig. 1). Our results show that *G. uralensis* sp. nov. differs significantly from *G. sibiricus* in many morphological characters (Fig. 9, Tables 3, 4) but is poorly distinguishable from the Caspian species *G. volgensis* (Fig. 9, Tables 3, 4). The latter, in turn, shares notable morphological similarities with *G. gobio* (Mendel et al. 2008). For this reason, gudgeons from the Ural basin were likely attributed to *G. volgensis* based on morphological analysis (Bogutskaya et al. 2013; Martynova and Vasil'eva 2021). The most reliable way to distinguish morphologically similar (or cryptic) species of the genus *Gobio* is through molecular genetic analysis (Mendel et al. 2008; this study). Based on DNA barcoding results, *G. uralensis* sp. nov. differs significantly from all other species of the genus, including the geographically neighboring *G. volgensis* (*p*-distance = 0.059 ± 0.009) and *G. sibiricus* (0.047 ± 0.008). At the same time, *G. uralensis* sp. nov. is genetically closer to Central Asian gudgeon species, namely *G. acutipinnatus* from the upper reaches of the Irtysh River (Ob' River basin; 0.037 ± 0.007) and *G. multipunctatus* from the Emel River in the Lake Alakol basin (0.037 ± 0.008) (see Table 1, Fig. 2).

Table 3. Morphometric characters for *Gobio* spp. (including the type series for *G. uralensis* sp. nov.) from three neighboring basins – range (mean ± standard deviation). Significant differences ($p < 0.05$) between populations are indicated with different lowercase letters (the non-parametric Kruskal-Wallis test followed by the Dunn's post hoc test). Green color shows the significant differences between *G. uralensis* sp. nov. and *G. volgensis*, yellow color shows significant differences between *G. uralensis* sp. nov. and *G. sibiricus*, and blue color shows significant differences between *G. uralensis* sp. nov., *G. volgensis*, and *G. sibiricus*.

Character	*G. volgensis* (n = 46)	*G. uralensis* sp. nov. (n = 77)	*G. sibiricus* (n = 37)
In percent of SL:			
Head length (HL)	25.3–29.7 (27.8 ± 1.04)[a]	25.6–30.0 (27.9 ± 1.10)[a]	26.9–30.9 (28.6 ± 0.94)[b]
Body depth at dorsal–fin origin	17.0–22.0 (19.2 ± 1.23)[a]	17.4–23.7 (19.8 ± 1.31)[a]	19.3–25.3 (22.6 ± 1.32)[b]
Caudal peduncle depth	7.6–9.5 (8.4 ± 0.43)[a]	7.2–8.8 (8.1 ± 0.40)[b]	8.9–10.9 (9.9 ± 0.50)[c]
Body width at dorsal–fin origin	11.6–16.6 (13.8 ± 1.23)[a]	12.7–17.8 (14.8 ± 1.17)[b]	13.3–19.0 (15.7 ± 1.35)[b]
Width of caudal peduncle at posterior anal–fin ray	6.1–9.5 (7.7 ± 0.90)	6.6–9.2 (7.7 ± 0.68)	6.7–9.2 (7.9 ± 0.72)
Predorsal length	42.2–51.5 (49.2 ± 1.50)[a]	47.4–52.6 (50.5 ± 1.30)[b]	48.8–53.5 (51.5 ± 1.09)[b]
Postdorsal length	38.2–44.4 (40.8 ± 1.47)[a]	36.3–42.1 (39.4 ± 1.22)[b]	37.6–42.6 (40.0 ± 1.28)[ab]
Prepelvic length	49.0–53.2 (51.0 ± 1.17)[a]	49.9–56.8 (52.0 ± 1.43)[b]	49.8–54.4 (52.2 ± 1.32)[b]
Preanal length	67.3–75.1 (71.8 ± 1.53)[a]	70.2–75.2 (73.0 ± 1.21)[b]	71.2–82.0 (74.4 ± 2.15)[c]
Distance between pectoral and pelvic–fin origins	20.6–26.6 (24.4 ± 1.40)	21.7–29.0 (25.2 ± 1.40)	23.1–27.1 (24.7 ± 1.28)
Distance between pelvic and anal–fin origins	18.9–24.0 (21.4 ± 1.13)[a]	19.3–25.1 (21.5 ± 1.23)[a]	19.9–23.8 (22.3 ± 1.08)[b]
Distance between anus and anal–fin origin	5.9–9.8 (7.9 ± 0.97)	5.5–9.5 (7.6 ± 0.85)	5.5–9.0 (7.6 ± 0.80)
Length of caudal peduncle	18.6–22.9 (20.8 ± 1.04)[a]	16.3–22.8 (19.6 ± 1.27)[b]	17.0–21.8 (18.6 ± 1.13)[c]
Dorsal–fin base length	10.6–14.7 (12.8 ± 0.83)[a]	11.8–14.6 (13.1 ± 0.73)[ab]	11.2–14.8 (13.4 ± 0.77)[b]
Dorsal–fin depth	18.9–23.3 (21.6 ± 1.12)[a]	18.2–23.1 (21.1 ± 1.08)[a]	20.72–25.34 (23.4 ± 1.31)[b]
Anal–fin base length	6.7–9.3 (7.5 ± 0.60)[a]	6.7–9.9 (8.0 ± 0.67)[b]	7.6–9.8 (8.6 ± 0.49)[c]
Anal–fin depth	13.6–18.2 (16.0 ± 0.87)[a]	14.9–18.0 (16.2 ± 0.78)[a]	16.1–19.9 (18.0 ± 0.94)[b]
Pectoral fin length	17.3–23.5 (20.5 ± 1.30)[a]	17.5–22.1 (19.8 ± 1.12)[a]	19.5–24.3 (22.0 ± 1.17)[b]
Pelvic fin length	1.2–17.6 (16.0 ± 2.36)[a]	13.9–17.5 (15.9 ± 0.82)[a]	16.1–20.2 (17.8 ± 0.85)[b]
In percent of HL:			
Head depth at nape	48.6–62.7 (56.0 ± 3.15)[a]	52.6–62.0 (56.5 ± 2.09)[a]	55.9–62.4 (59.6 ± 1.88)[b]
Head depth at eye	40.9–54.5 (48.2 ± 2.81)	43.4–54.9 (48.2 ± 3.08)	45.3–51.2 (49.1 ± 1.69)
Snout length	33.6–48.4 (43.1 ± 2.72)[a]	40.9–48.8 (44.8 ± 2.01)[b]	39.6–47.0 (43.4 ± 1.86)[a]
Eye diameter	18.3–26.6 (21.1 ± 1.59)	17.6–25.2 (21.0 ± 1.82)	18.9–22.9 (21.1 ± 1.05)
Postorbital distance	35.9–43.4 (40.8 ± 1.63)[a]	38.8–46.7 (41.5 ± 1.87)[ab]	38.2–45.2 (42.4 ± 1.92)[b]
Maximum head width	49.1–65.3 (58.3 ± 3.20)[a]	51.8–66.4 (59.0 ± 3.05)[a]	57.0–67.6 (61.8 ± 3.02)[b]
Interorbital width	21.4–31.3 (25.8 ± 2.23)[a]	22.3–29.6 (25.9 ± 1.56)[a]	27.9–33.0 (30.4 ± 1.45)[b]
Barbel length	20.2–30.0 (24.7 ± 2.37)[a]	15.9–32.6 (24.7 ± 3.28)[a]	22.4–35.5 (27.7 ± 3.89)[b]
Ratios:			
Interorbital width/eye diameter	1.0–1.6 (1.2 ± 0.16)[a]	1.0–1.5 (1.2 ± 0.13)[a]	1.2–1.6 (1.4 ± 0.11)[b]
Snout length/eye diameter	1.6–2.5 (2.1 ± 0.23)	1.7–2.6 (2.2 ± 0.21)	1.8–2.4 (2.1 ± 0.13)
Head depth at nape/eye diameter	2.1–3.2 (2.7 ± 0.24)[a]	2.2–3.3 (2.7 ± 0.28)[ab]	2.5–3.1 (2.8 ± 0.17)[b]
Caudal peduncle length/depth	2.1–2.9 (2.5 ± 0.18)[a]	2.0–2.8 (2.4 ± 0.19)[a]	1.6–2.3 (1.9 ± 0.15)[b]

The range of the Ural gudgeon remains uncertain. Currently, its distribution is reliably defined only for the localities sampled in this study. We assume that *G. uralensis* sp. nov. may be distributed throughout the entire Ural River basin, including the Kazakhstan's part of the basin.

It is noteworthy that the small genetic distance between *G. acutipinnatus* and *G. multipunctatus* (0.004 ± 0.002) (see Table 1, Fig. 2) suggests that they may represent different populations of the same species. This issue can be clarified through molecular analysis, including specimens of *G. acutipinnatus* from its type locality, Lake Markakul. The specimens previously identified as *G. acutipinnatus* (Yang et al. 2016; Yi and Fu 2020) are from the Chinese section of the Irtysh River and may actually refer to a different species – possibly the recently described *G. multipunctatus*. Moreover, according to the study describing *G. multipunctatus* (Vasil'eva et al. 2023), this species is not native to the Lake Alakol basin in Kazakhstan, although it was originally described from that region. This reflects a broader issue: the ongoing introduction and establishment of alien species in Kazakhstan, including in the Lake Alakol basin (Mamilov et al. 2015, 2022, 2024; Sharakhmetov 2022). Thus, the taxonomic status of the gudgeons inhabiting the Central Asian region remains unclear and requires further research.

Gobio uralensis sp. nov. is genetically closer to the geographically distant *G. acutipinnatus* and *G. multipunctatus* (see Fig. 1), that is likely explained by paleogeographic factors and ancient hydrological connections between the Ural and Irtysh river basins. Several basins are between these riverine systems, including the Nura and Sarysu rivers, the rivers and water bodies of the Irgiz-Turgai trough, the Emba and Uil rivers, and numerous smaller lake and river systems. Most of these are currently endorheic (drainless), but during high-water years, they may overflow into the Ob' or Caspian Sea basins (Davydov 1936). Part of these modern basins was, during the Late Pliocene and Pleistocene, composed of glacial-sub-

Table 4. Meristic characters of the studied *Gobio* spp. Significant differences ($p < 0.05$) between populations are indicated with different lowercase letters (the non-parametric Kruskal-Wallis test followed by the Dunn's post hoc test). Green color shows significant differences between *G. uralensis* sp. nov. and other *Gobio* species. Abbreviations: lim – limits; M – mean; SD – standard deviation.

Characters	K-U	*G. acutipinnatus* (n = 10)			*G. sibiricus* (n = 37)			*G. uralensis* sp. nov. (n = 77)			*G. volgensis* (n = 46)		
	p	lim	M	SD	lim	M	SD	lim	M	SD	lim	M	SD
D	0.441	7–7	7.0	0.00	7–7	7.0	0.00	7–8	7.0	0.11	7–8	7.0	0.21
A	0.441	6–6	6.0	0.00	6–6	6.0	0.00	6–6	6.0	0.00	5–6	6.0	0.15
P	0.00257*	13–16	14.4^{a}	0.84	14–17	15.0^{ab}	0.69	13–17	15.3^{b}	0.91	13–17	15.4^{b}	0.66
V	0.0604	7–7	7.00	0.00	7–8	7.0	0.11	5–8	7.0	0.29	7–8	7.2	0.31
LL	<0.0001*	37–42	38.6^{ab}	0.98	36–40	37.8^{a}	0.82	36–42	38.9^{b}	0.93	37–42	38.9^{b}	0.85
LLt	<0.0001*	40–44	41.6^{a}	0.89	40–43	41.3^{a}	0.80	39–45	42.1^{b}	0.86	41–45	42.6^{c}	0.84
up LL	<0.0001*	5–7	5.6^{ab}	0.53	5–6	5.5^{a}	0.46	4–6	5.5^{a}	0.46	5–6.5	5.9^{b}	0.27
down LL	0.0133*	3–5	4.0^{a}	0.24	3–4	3.7^{ab}	0.38	3–5	3.6^{b}	0.47	3–4.5	3.8^{ab}	0.32
CPS	0.0341*	11–15	12.6^{ab}	1.17	12–14	12.3^{a}	0.58	11–15	12.6^{ab}	0.85	12–15	12.9^{b}	0.93
Blotches on flank	0.313	9–11	10.2	0.67	7–11	8.2	0.83	6–14	9.6	1.30	7–12	9.2	0.88
GR	0.109	–	–	–	3–5	3.7	0.67	2–5	3.8	1.20	2–5	3.2	0.73
Vert.	0.000974*	40–41	40.1^{ab}	0.38	39–41	39.9^{a}	0.64	39–42	40.30^{b}	0.67	40–42	40.5^{b}	0.66
Va	0.152	21–22	21.1	0.38	20–22	21.0	0.58	20–22	21.0	0.56	20–22	21.2	0.47
VpreD	0.00592*	11–12	11.3^{ab}	0.49	10–12	11.2^{a}	0.53	11–13	11.6^{b}	0.54	10–12	11.4^{ab}	0.55
Vi	0.736	3–5	3.9	0.69	3–5	4.1	0.52	3–5	4.0	0.71	3–5	4.0	0.71
Vc	0.0101*	18–20	19.0^{ab}	0.58	18–20	18.9^{a}	0.60	18–21	19.3^{b}	0.65	18–21	19.3^{b}	0.56
VpreA	0.599	2–3	2.1	0.38	1–3	2.0	0.69	1–3	1.9	0.50	1–3	1.9	0.58
VpostA	0.00173*	16–18	16.9^{ab}	0.69	16–18	17.0^{a}	0.70	16–19	17.4^{b}	0.65	16–19	17.5^{b}	0.62

Figure 6. Type locality of *Gobio uralensis* sp. nov. – Bolshoy Kizil River near Ryskuzhino (53.3161°N, 58.3351°E, 24 Aug. 2020).

pond lake and riverine systems that were repeatedly connected via the Irgiz-Turgai trough, facilitating two-way flow between the Ob' and Caspian Sea basins (Kvasov 1975; Grosswald 1999). Paleohydrological connections might facilitate the historical dispersal of ancestral gudgeon lineages, followed by geographical isolation. At present, no genetic data are available for gudgeons inhabiting the water bodies of the Irgiz-Turgai trough. It is possible that gudgeons belonging to lineages closely related to *G. uralensis* and *G. acutipinnatus* inhabit or formerly inhabited other water bodies in southern Siberia and northern Central Asia, between Lake Markakol and the Ural basin.

Faunistic relationships between the Arctic Ocean and Caspian Sea basins have been a subject of zoological interest since the work of Berg (1928). Makhrov et al. (2020) summarized recent data and demonstrated, using multiple examples, that faunal exchanges between these basins have occurred in both directions and at various times. We provide examples of faunal dispersal between the Caspian Sea and Siberian river basins – particularly the Ob' River and its tributary, the Irtysh River – as the gudgeons examined in this study exhibit a similar pattern of past dispersal. The so-called *baerii*-like mitotype (similar to the mtDNA haplotypes of the Siberian sturgeon *Acipenser baerii* Brandt, 1869) was detected in approximately 30% of Russian sturgeons (*Acipenser gueldenstaedtii* Brandt, 1833; Acipenseriformes: Acipenseridae) from the North Caspian basin (Ural and Volga rivers) (Birstein et al. 2000; Jenneckens et al. 2000; Timoshkina et al. 2009). Water bodies in the southwestern Irtysh basin are inhabited by gastropod mollusks of Ponto-Caspian origin – the genus *Caspiohydrobia* Starobogatov, 1970 (Gastropoda: Hydrobiidae) (Andreeva 1987). Bivalves of the genus *Unio* Philipsson, 1788 (Bivalvia: Unionidae), recorded in the upper Irtysh basin and its tributary, the Uy River, likely reflect the presence of a refugium in the upper reaches of the basin, further supporting the hypothesis of ancient faunal exchange between the Caspian and Ob' basins (Andreeva et al. 2009; Bolotov et al. 2020). The vectors and timing of ancient aquatic animal dispersal remain incompletely understood. It is assumed that the ancestor of the Siberian sturgeon (*A. baerii*) colonized Siberian rivers from the Ponto-Caspian basin (Birstein and DeSalle 1998; Birstein et al. 2000), later surviving glaciation in a refugium, presumably Lake Baikal (Barmintseva and Mugue 2017), where it speciated. A subsequent recolonization of the Caspian basin by *A. baerii* likely occurred during one of the last Pleistocene glacial-interglacial cycles (Timoshkina et al. 2009). The mollusks *Caspiohydrobia* and *Unio* also clearly have Caspian origins upon colonizing the Irtysh basin (Makhrov et al. 2020).

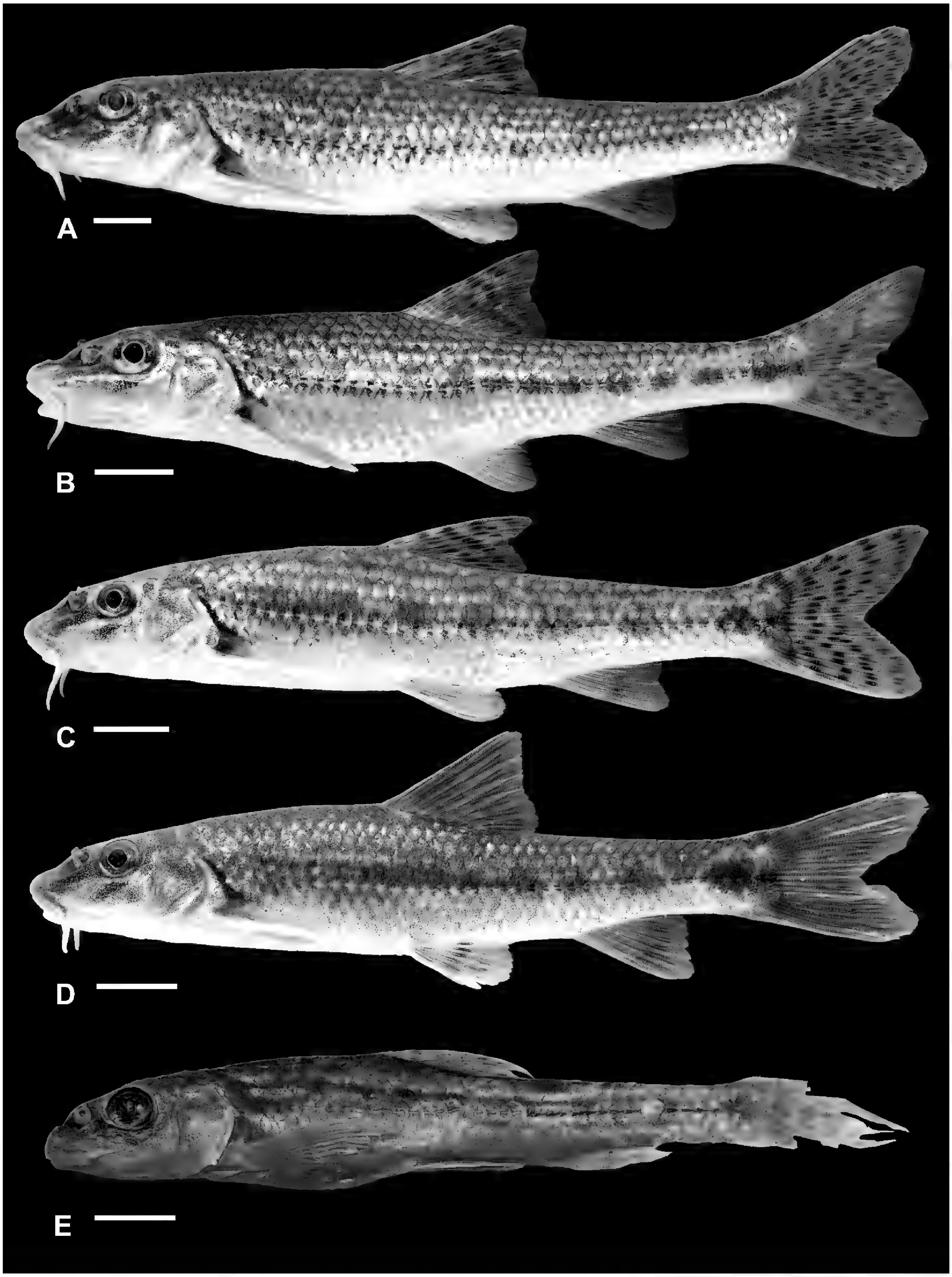

Figure 7. Lateral view of *Gobio* spp. (comparative material): **A, B.** *G. volgensis* (**A.** Chusovaya River near Kosoy Brod; **B.** Buzuluk River near Fedorovka (right side, inverted image)); **C, D.** *G. sibiricus* (**C.** Koelga River near Zvyagino; **D.** Sinara River near Bulzi), **E.** *G. acutipinnatus*, syntype ZISP 26865 (Lake Markakol). **A–D.** Live coloration; **E.** Preserved specimen of 1936 year. Scale bar: 10 mm.

In contrast, reverse colonization is exemplified by the Siberian taimen *Hucho taimen* (Pallas, 1773) (Salmoniformes: Salmonidae), which entered the Caspian basin from Siberia in the Late Pleistocene, likely via paleohydrological connections through the Chusovaya River (Marić et al. 2014), originating in Siberia. The Chusovaya River has served as a bi-directional corridor for faunal exchange between Europe and Asia, as seen from

Figure 8. Breast and belly view of *Gobio* spp.: **A.** *G. uralensis* sp. nov., Ural River near Krasnogor; **B.** *G. volgensis*, Schegrinka River near Jidobuzhi; **C.** *G. sibiricus*, Koelga River near Zvyagino. Scale bar: 10 mm.

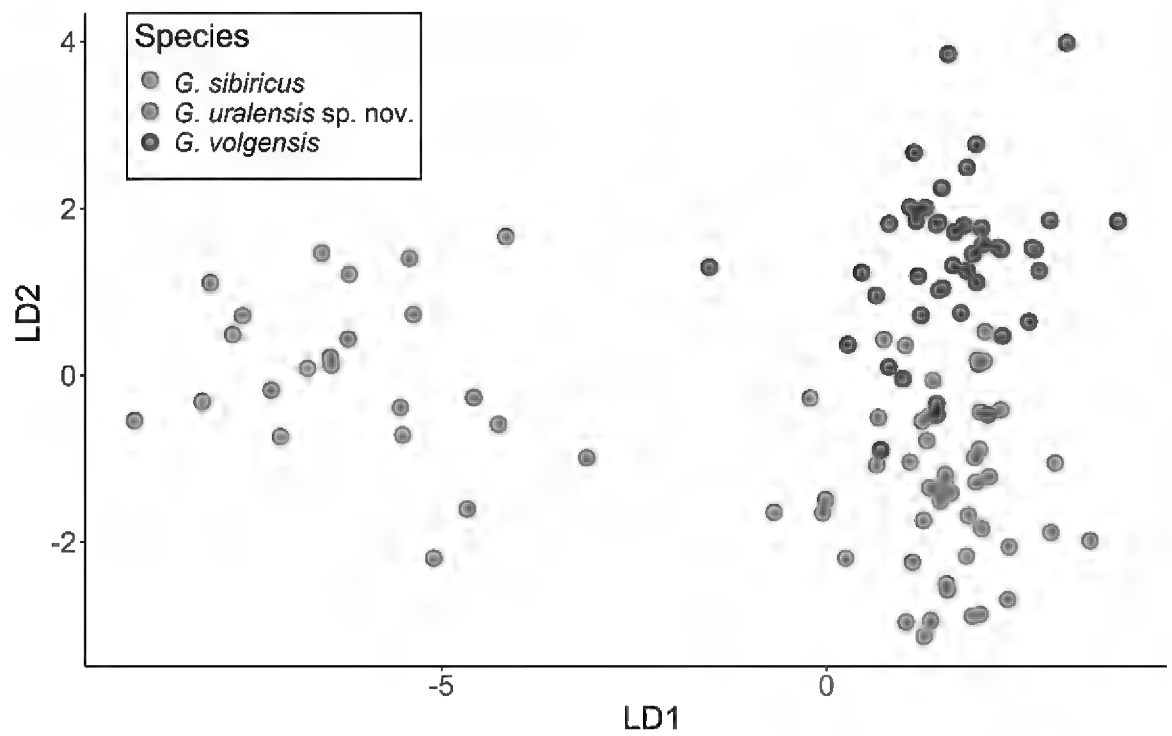

Figure 9. Linear Discriminant Analysis (LDA) of *Gobio uralensis* sp. nov. (n = 77), *G. volgensis* (n = 46), and *G. sibiricus* (n = 37) based on 31 morphometric indexes and ratios.

the Northern minnow *Phoxinus isetensis* (Georgi, 1775) (Cypriniformes: Leuciscidae), which migrated from the Caspian to the Ob' basin (Artaev et al. 2024). An issue on the route of colonization of the Ural River basin by the proto-lineage of *G. uralensis* sp. nov. is still unclear.

In summary, our study demonstrates that the Ural River – a major river forming the boundary between Europe and Asia – is inhabited by an endemic gudgeon species, here described as *G. uralensis* sp. nov. Notably, *G. uralensis* sp. nov. is the only endemic fish species known from the Ural River basin. To better understand the evolutionary origin of the Ural gudgeon and the zoogeographic relationships between Asia and Europe, it is essential to clarify the phylogenetic affinities and taxonomic status of *Gobio* species inhabiting the region of historic paleohydrological connections between the Ob' and Caspian Sea basins – specifically, the Nura and Sarysu rivers, the Irgiz-Turgai trough, and the Emba and Uil rivers. However, genetic data on fish from this region are currently limited (see Suppl. material 1).

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Supplementary material 1

Material for genetic studies

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Data type: xlsx

Link: https://doi.org/10.3897/zse.101.147368.suppl1

Supplementary material 2

The best partition schemes generated by ModelFinder v.2.2.0 (ML) and PartitionFinder v.2.1.1 (BI)

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Data type: docx

Link: https://doi.org/10.3897/zse.101.147368.suppl2

Supplementary material 3

ML phylogenetic tree of COI mtDNA sequences representing all available species in GenBank combined with our data set

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Data type: docx

Link: https://doi.org/10.3897/zse.101.147368.suppl3

Supplementary material 4

Coefficients of linear discriminants based on LDA

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